

The Columbariinae (Gastropoda: Turbinellidae) of the eastern Indian Ocean

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ABSTRACT

The occurrence of the subfamily Columbariinae in the eastern Indian Ocean is documented for the first time. Of the 5 species recognized, one, *Coluzea distephanotis*, new combination, has been previously described from the Torres Strait. Additional material suggests that this type locality is erroneous. Four new species, *Coluzea aapta*, *C. icarus*, *C. liriopae* and *C. gomphos* are described. The eastern Indian Ocean species appear to be more closely related to their congeners from off southern and eastern Africa than to those from off New Zealand, suggesting post-Eocene vicariance of at least some elements of the psychrospheric faunas of the Indian and Pacific Oceans.

INTRODUCTION

The subfamily Columbariinae is represented in the Recent fauna by about 50 species that inhabit areas of the outer continental shelf and upper continental slope. This group, until recently accorded family status, has been reduced to a subfamily of Turbinellidae on the basis of radular, anatomical and dietary data (Harasewych, 1983). The subfamily first appeared in the Late Cretaceous (Maastrichtian) of Europe, and by Paleocene time ranged from North America to New Zealand. These as well as Eocene records are from shallow water facies, while the few post-Eocene records are limited to the deep water facies of southeastern Australia and New Zealand (Darragh, 1969; Finlay, 1930). The shift of the group to deeper water occurred at about the time of formation of the psychrosphere, the lower, cold ($<10^{\circ}\text{C}$) layer of a two layer ocean (Bruun, 1957; Benson, 1975; Corliss, 1979). The few temperature records available indicate that Recent species live below the 10°C thermocline.

In the Recent fauna, the subfamily is well represented in the western Atlantic (Bayer, 1971; Harasewych, 1983), western Indian (Tomlin, 1928; Barnard, 1959; Darragh, 1969) and western Pacific (Habe, 1979; Darragh, 1969; Powell, 1979) Oceans. A single, wide ranging species was recently discovered in the eastern Pacific (McLean and Andrade, 1982). Deep water trawling by the Australian Commonwealth Scientific and Industrial Organization (CSIRO) has yielded 55 specimens of

columbarines from off northern Western Australia. This material, together with additional specimens located in the collections of European and American museums, serves as the basis for this report.

MATERIALS AND METHODS

I was fortunate in being able to examine most specimens of Columbariinae taken in the eastern Indian Ocean, including preserved or dried animals of 4 of the 5 species recognized herein. Specimens for anatomical studies were extracted from their shells or, in several cases, the shells were dissolved in 10% hydrochloric acid (HCl), the animals rinsed in distilled water and dissected in 70% ethanol. In order to determine gut contents, a section of rectum was excised, transferred to a microscope slide, teased apart and examined. Several drops of bleach (5% sodium hypochlorite) were then added to dissolve organic material. After 20 minutes, the sample was diluted with distilled water, filtered through a 0.45 μm membrane filter, rinsed, dried and examined under SEM. Scanning electron micrographs were taken using a Hitachi S-570 SEM.

Specimens of the 5 species discussed herein, as well as of *Coluzea spiralis* (A. Adams, 1856) [DMNH 48393, 73077] from the Recent of New Zealand and *Coluzea serrata* (Deshayes, 1825) [BM(NH)PD 31640] from the Paris Basin Eocene were scored for the 12 characters listed in table 1. The mean values of the characters formed the data matrix for the phenetic analyses. The standardized data (mean = 0, standard deviation = 1) were used to calculate a Euclidian distance matrix and phenograms based on UPGMA and single linkage (nearest neighbor) clustering were produced using the PHYSYS program (Farris and Mickevich, 1985).

The repositories of examined specimens are indicated by the following abbreviations:

- ANSP — Academy of Natural Sciences, Philadelphia.
- BM(NH)PD — British Museum (Natural History) Paleontology Dept.
- DMNH — Delaware Museum of Natural History
- MM — Manchester Museum
- MNHN — Museum National d'Histoire Naturelle, Paris
- USNM — National Museum of Natural History, Smithsonian Institution
- WAM — Western Australian Museum
- ZMUC — Zoological Museum, University of Copenhagen

Table 1. Shell characters used in phenetic analyses. Characters 1 through 8 describe the geometry of the generalized shell form (Harasewych, 1982).

1. Shape of the generating curve of the body cavity (Sbc).
2. Shape of the generating curve of the siphonal canal (Ssc).
3. Relative siphonal length (Rsl).
4. Siphonal angle (beta).
5. Angle of the generating curve (theta).
6. Rate of whorl expansion (W).
7. Position of the generating curve relative to the axis (D).
8. Rate of whorl translation (T).
9. Number of varices/spines on final whorl (# var.).
10. Distance from periphery to rim/distance from periphery to suture (rim).
11. Pigmentation on shell: present 0, absent 1, (color).
12. Spines on periphery: closed 0, open 1, (spines).

SYSTEMATICS

Family TURBINELLIDAE Swainson, 1840
 Subfamily COLUMBARIINAE Tomlin, 1928
 Genus COLUZEA Allan, 1926



PLATE 1

1-4. *Coluzea distephanotis* (Melvill, 1891). 1. WAM 1632-84, NW of Cape Leveque, Western Australia, 302-300 m, 0.6 X. 2. Holotype, Manchester Museum EE 3651, Chalmondeley Collection. Torres Strait, 17 fathoms, 1.5 X. 3. WAM 3273-84, SW of Imperieuse Reef, Rowley Shoals, Western Australia, 355-356 m, 0.6 X. 4. Protoconch of holotype, 15 X. 5-8. *Coluzea aapta* new species. 5. Holotype, WAM 1089-84, NW of Beagle Bay, Western Australia, 504-500 m, 0.6 X. 6. Paratype 1 USNM 859030, NW of Beagle Bay, Western Australia, 504-500 m, 0.6 X. 7. WAM 1095-84, NW of Cape Leveque, Western Australia, 500-506 m, 0.6 X. Arrows indicate anemones. 8. Protoconch of paratype 1, 15 X.

Coluzea Allan, 1926, Trans. N.Z. Inst. 57:304, issued separately December 7, 1926. Type species: *Fusus dentatus* Hutton, 1877, by monotypy.

Coluzea Finlay, 1927, Trans. N.Z. Inst. 57:407. Type species: *Fusus spiralis* A. Adams, 1856, by original designation.

Of the seven supraspecific taxa included within Columbariinae, most have been regarded at one time or another as genera (Darragh, 1969) or subgenera (Bayer, 1971), and higher systematics within the subfamily is still tentative. In a previous paper (Harasewych, 1983) I recognized the genera *Columbarium* and *Fulgurofusus*, and provisionally considered *Coluzea* to be a subgenus of the latter. Although *Coluzea* is closer to *Fulgurofusus* than to *Columbarium* in shell and radular morphology, it is retained as a genus level taxon until a revision of the subfamily can be completed.

Earliest records of *Coluzea* date back to the Middle-Eocene of Europe. The present range spans the Indian and southwestern Pacific Oceans.

Columbarium distephanotis Melvill, 1891, J. Conch. London 6(12): 405, pl. 2, fig. 4.

Columbarium distephanotis Melvill. Darragh, 1969. Proc. Roy. Soc. Vict. 83(1): 85, pl. 4, figs 58, 64.

***Coluzea distephanotis* (Melvill, 1891)**

Plate 1, figs 1-4; Plate 3, fig. 1

Description:

Shell:

Large for genus (to 78 mm), moderately heavy, fusiform; spire angle 32°-37°; protoconch (pl. 1, fig. 4) with 1½ glassy, bulbous whorls; transition to teleoconch gradual, marked by increase in coarseness of growth striae and development of peripheral keel that becomes nodulose then spinose, with 11-13 short, open spines on second post-nuclear whorl; teleoconch with up to 9½ strongly convex whorls; suture adpressed; strong spiral cord anterior to periphery appears by second post-nuclear whorl, forming double keel prominent on early whorls but diminished by eighth post nuclear whorl; area between suture and periphery smooth or with up to 6 weak spiral cords; 2-4 strong spiral cords between periphery and anterior carina, 3-4 between anterior carina and siphonal canal, 18-28 along posterior ⅔ of siphonal canal, with 0-3 fine threads between adjacent spiral cords; axial sculpture of 12-16 short open spines along periphery, expanding basally to form abbreviated ribs along double keel; aperture ovate; outer lip thick, furrowed beneath periphery; inner lip smooth, procelaneous; siphonal canal long, axial, stout, distal ½ may be sinuate; shell color uniformly white; periostracum short, thin, axially-bladed, straw-colored.

Ultrastructure:

Shell consists of 2 orthogonal layers of crossed-lamellar aragonite; outer layer, with lamellar planes parallel to growing edge, comprises surface sculpture and varies in thickness; inner layer, with lamellar planes perpendicular to growing edge, more uniform in thickness (200-400 µm), thickest at periphery and juncture with siphonal canal.

Animal:

A single, poorly-preserved, male specimen (USNM 859029) was dissected. Mantle cavity spanned ¾ whorl, kidney ½ whorl, upper whorls not preserved; foot long, broad, with strongly ovate, amber-colored terminally-nucleated operculum; tentacles short, blunt, with very small black eyes; mantle edge thickened, papillose; osphradium long, narrow (L/W = 3.9), with 66 filaments/side; ctenidium 2.2 times as wide as osphradium, nearly twice as long; hypobranchial gland very large, deep, transversely pleated; rectum long, narrow, with short anal gland; proboscis long (about ⅔ shell length), narrow; radula (pl. 3, fig. 1) short (3.2 mm), narrow (150 µm), with 126 rows of teeth; lateral teeth with single, scythe-shaped cusp; rachidian tricusped, basal plate crescent-shaped with expanded ends; salivary glands large, asymmetrical; gland of Leiblein large, displaced to left side of cephalic hemocoel by proboscis sheath; male pallial gonoduct with large prostate gland along posterior ⅓ of mantle cavity, descending to floor of mantle cavity to form muscular open groove that runs anteriorly and along inner edge of broad, flattened penis.

Etymology:

Gr. *di* — two + Gr. *stephanos* — a wreath or crown of leaves.

Type specimen:

Holotype — Manchester Museum EE 3651, Chalmondeley Collection, length 18.9 mm.

Type locality:

Dredged off the south shores of New Guinea, Torres Straits, in 17 fathoms (31 m).

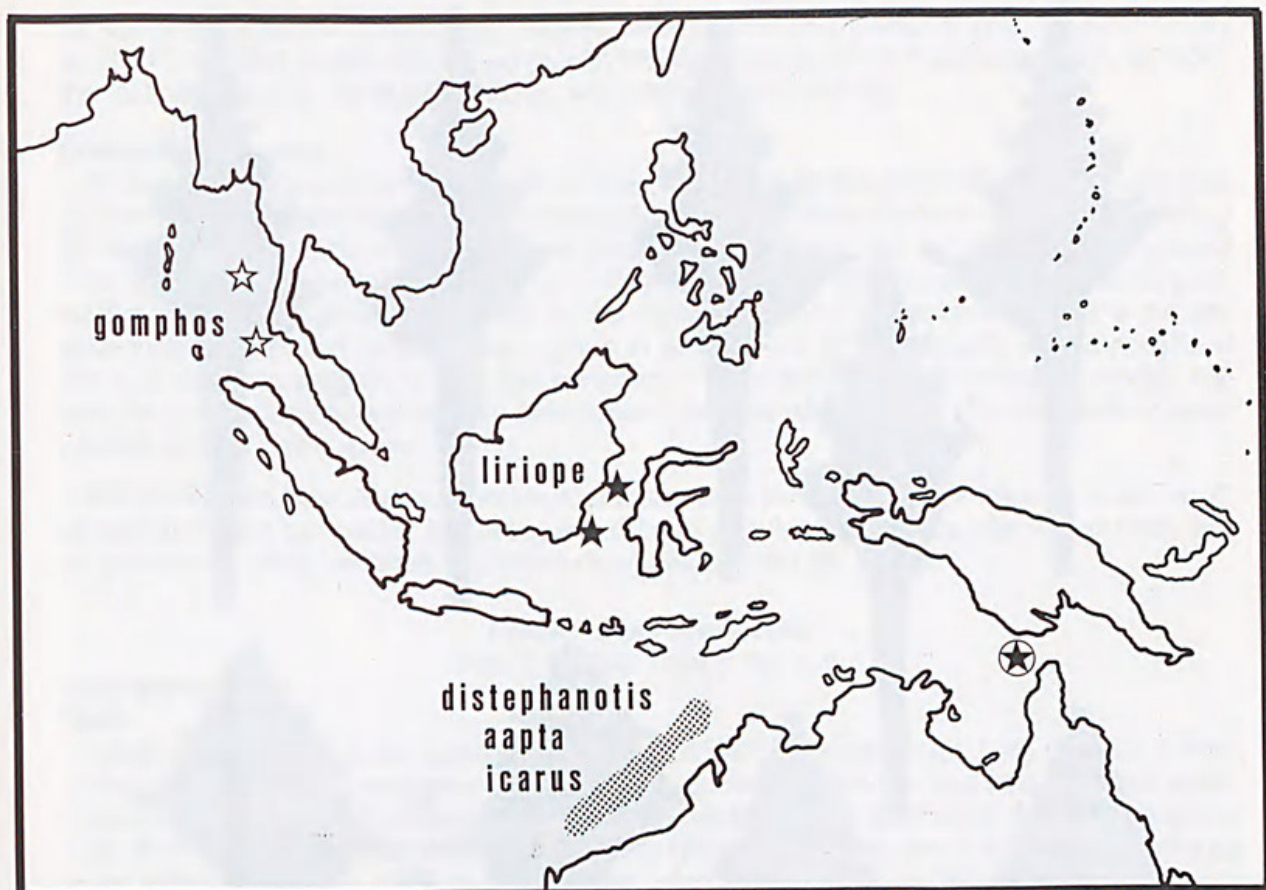


Figure 1. Geographic distribution of eastern Indian Ocean species of *Coluzea*. Circled star marks type locality of *C. distephanotis*.

Distribution (fig. 1):

This species inhabits the upper continental slope off northern Western Australia in depths of from 300–444 m, with a mean station depth ($n = 10$) of 363 m. The type locality, Torres Straits, in 31 m, is regarded as dubious, since it is well out of the bathymetric range of other records not only for this species, but for the subfamily. The holotype is in very good condition, precluding extensive transport after death. In the original description, Melvill (1891: 405) notes “it has all the appearance of molluscs procured from abysmal depths.”

Ecology:

Coluzea distephanotis occurs on bottoms ranging from sand and coral rubble to fine mud at depths from 300 to 444 m, with records from depths greater than 360 m based on dead and worn specimens. Rectal contents include large numbers of polychaete setae. Almost all specimens have repaired breaks along the proximal portion of the siphonal canal suggesting heavy crab predation. Four of 18 specimens have large naticid bore holes, all 1 to 1½ whorls above the aperture.

Material examined:

Off south shores of New Guinea, Torres Straits, dredged in 31 m (Manchester Museum EE 3651 — holotype); SW of Imperieuse Reef, Rowley Shoals, Western Australia, 18°05'S, 118°10'E, in 400–401 m, mud (WAM 3259-83); SW of Imperieuse Reef, Rowley Shoals, WA, 18°06' 118°10'E, in 355–356 m, mud (WAM 3273-83); SW of Imperieuse Reef, Rowley Shoals, WA, 18°08'S, 118°13'E, in 300–354 m, mud (USNM 859029); NW of Beagle Bay, WA 15°20.0'S, 121°09.6'E to 15°18.0'S, 121°11.2'E, in 300–302 m, rubble (WAM 1613-84); NW of Cape Leveque, WA, 14°49.0'S, 121°36.1'E to 14°58.8'S, 121°35.6'E, in 302–300 m, soft mud (WAM 1632-84); NW of Collier Bay, WA, 14°16.5'S, 122°34.4'E to 14°13.6'S, 122°38.3'E, in 302 m, sand and coral rubble (WAM 1771-84); NW of Augustus Island, WA, 13°27.6'S, 122°44.6'E to 13°25.0'S, 122°47.0'E, in 444–440 m, sand and rock rubble (WAM 1781-84); WNW of Lacepede Archipelago, WA, 15°21.2'S, 120°44.3'E to 15°49.3'S, 120°45.3'E, in 350–348

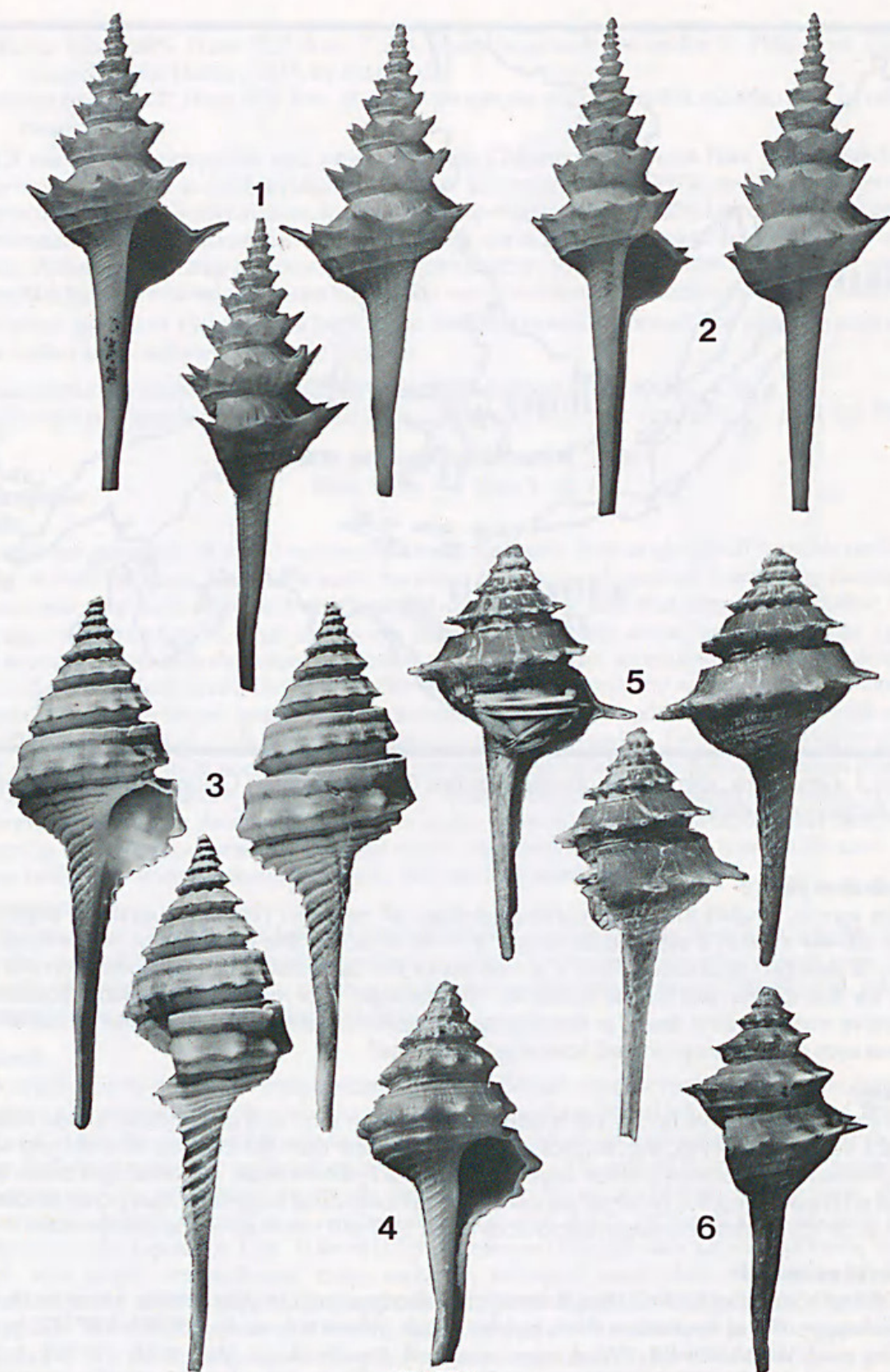


PLATE 2

1-2. *Coluzea icarus* new species. 1. Holotype, WAM 1784-84, NW of Augustus Island, Western Australia, 494-484 m, 0.6 X. 2. Paratype 1, USNM 859031, NW of Augustus Island, Western Australia, 494-484 m, 0.6 X. 3-4. *Coluzea liriopoe* new species. 3. Holotype ZMUC, SW Makassar Strait, in 585 m, 1.0 X. 4. MNHN, NW Makassar Strait, in 595 m, 1.1 X. 5-6. *Coluzea gomphos* new species. 5. Holotype, ANSP 29183, 75 miles ESE of Phuket, Thailand, in 512-503 m, 1.5 X. 6. ANSP 291969, 77 miles W of Clara Island, Burma, in 384 m, 0.8 X.

m, soft bottom (WAM 1788-84); 127 nautical miles NW of Port Hedland, WA, 18°26'S, 117°34'E to 18°24'S, 117°36'E, in 418-416 m, mud (WAM 925-85); W of Lacepede Archipelago, WA, 16°56.9'S, 119°52'E to 16°55.8'S, 119°53.8'E, in 432 m, soft bottom (WAM 929-85)

Comparative remarks:

Coluzea distephanotis most closely resembles *Coluzea cingulata* (Martens, 1901), known only from the holotype taken in 818 m off Tanzania, East Africa. Both are similar in general morphology of shell and protoconch, and both have a double keel composed of the periphery and a spiral cord anterior to the periphery. While in *C. distephanotis* the keel appears by the second post-nuclear whorl and is greatly diminished by the eighth whorl, in *C. cingulata* it appears in the fifth post-nuclear whorl and continues to increase in prominence. In *C. cingulata*, the subperipheral rim is as or more prominent than the periphery, and axial sculpture is limited to nodes. The periphery of *C. distephanotis* is more pronounced than the subperipheral rim, and axial sculpture consists of short, open spines.

Of the Recent New Zealand species, *Coluzea spiralis* (A. Adams, 1856) appears closest to *C. distephanotis* but can readily be distinguished by its angular protoconch, pigmented shell, lack of open spines along periphery and more elongated rachidia (pl. 3, fig.6).

Coluzea aapta new species

Plate 1, figs 5-8; Plate 3, figs. 3, 4.

Description:

Shell:

Large (to 73 mm), delicate, fusiform; spire angle 32°-40°; protoconch (pl. 1, fig. 8) of 1 ½ whorls, bulbous, pitted; transition to teleconch marked by formation of peripheral keel and axial nodes, followed within ½ whorl by appearance of spiral sculpture above and below the keel; periphery with 10-12 doublet nodes on second post-nuclear whorl that develop into 2 rows of perpendicular open spines numbering 12-16 on body whorl; teleoconch with up to 10 convex whorls; suture adpressed; area between suture and periphery with 6-8 weak spiral threads that decrease in prominence with increasing shell size; 2-4 weak spiral cords between periphery and anterior carina, 3-4 between anterior carina and siphonal canal and 20-28 along proximal ⅔ of siphonal canal, with 0-3 weak threads between adjacent cords; axial sculpture limited to nodes on early whorls and doublet spines along periphery; aperture strongly ovate to triangular; outer lip thin, furrowed beneath both rows of spines; inner lip smooth; siphonal canal long, thin, distally sinuate; shell color white within and without; periostracum very thin, with short axial blades.

Animal:

One female specimen (holotype WAM 1089-84) and one immature male specimen (paratype USNM 859030) were dissected. Body of about 2 ½ whorls, mantle cavity ¾ whorl, kidney, ½ whorl, digestive gland ¾ whorl; foot small, squarish, with strongly ovate, amber colored operculum; tentacles short, with very small black eyes; mantle edge thickened, papillose; osphradium short (L/W = 2.8), with 68 leaflets/side; ctenidium 1.6 times osphradium width, 2 times osphradium length; hypobranchial gland transversely pleated, deeply glandular; rectum long, narrow, with anal gland along anterior ⅓ of length; extended proboscis 1.6 times shell length, narrow (pl. 3, fig. 3); radula (pl. 3, fig. 4) short (3mm), narrow (220 µm), with 90-96 rows of teeth; lateral teeth monocusped; rachidia tricusped with laterally expanded basal plates; valve of Leiblein small; salivary glands asymmetrical; gland of Leiblein large, situated to left and below proboscis sheath; stomach u-shaped; male pallial gonoduct narrow, closed duct along posterior ⅓ of mantle cavity, descending to floor of mantle cavity to form open muscular groove leading to and running along the edge of a short, dorsoventrally flattened penis. Female pallial gonoduct of long, broad capsule gland and ovate bursa copulatrix.

Etymology:

Gr. *aaptos* — unapproachable. So named because of the long spines and zoanthid anemones that live on shells of live taken specimens.

Type material:

Holotype — WAM 1089-84, length 70.4 mm; paratypes 1-3 USNM 859030, lengths 54.9 mm, 57.6 mm, 58.1 mm; paratypes 4-7 WAM 1617-84, lengths 62.9 mm, 48.1 mm, 39.5 mm, 36.0 mm.

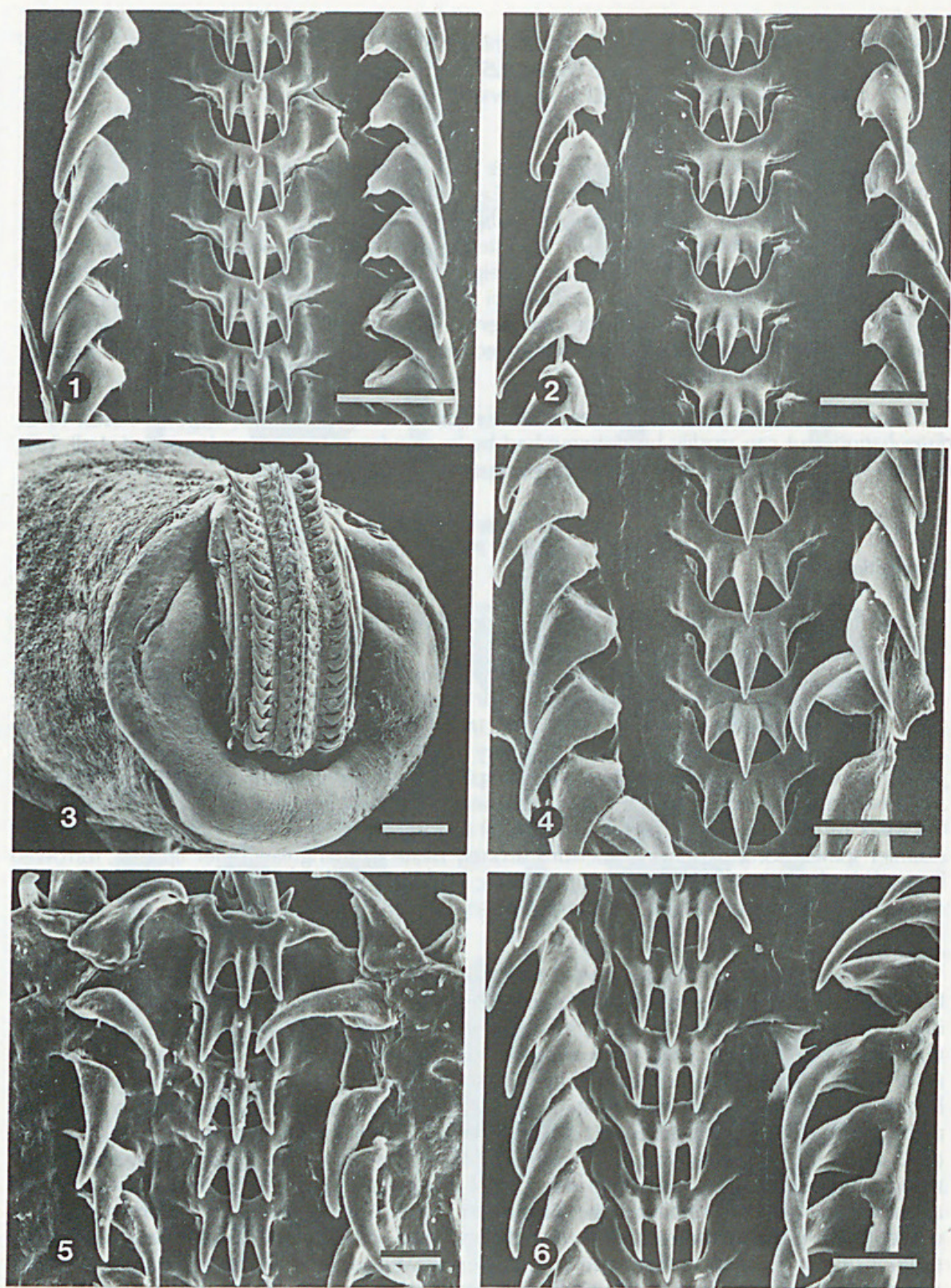


PLATE 3

Fig. 1. Radula of *Coluzea distephanotis* (Melvill, 1891), from specimen in plate 1, fig. 3 (WAM 3273-84). Scale bar = 50 μ m. Fig. 2. Radula of *Coluzea icarus* n. sp., from holotype (pl. 2, fig. 1, WAM 1784-84). Scale bar = 50 μ m. Fig. 3. Critical Point dried proboscis tip of *Coluzea aapta* n. sp., from specimen in plate 1, fig. 7 (WAM 1095-84). Scale bar = 150 μ m. Fig. 4. Radula of *Coluzea aapta* n. sp., from holotype (pl. 1, fig. 5; WAM 1089-84). Scale bar = 50 μ m. Fig. 5. Radula of *Coluzea liriopoe* n. sp. from holotype (pl. 2, fig. 4; ZMUC). Scale bar = 25 μ m. Fig. 6. Radula of *Coluzea spiralis* (A. Adams, 1856). DMNH 48393. Scale bar = 50 μ m.

Type locality:

NW of Beagle Bay, Western Australia 15°08.6'S, 121°03.4'E to 15°06.0'S, 121°06.6'E in 504-500 m.

Distribution (fig. 1):

Coluzea aapta inhabits the upper continental slope off northern Western Australia in depths from 348-600 m (\bar{x} = 499 m, n = 12).

Ecology:

All specimens of this species have been taken on mud bottoms at depths ranging from 348-600 m. The 348 m record is based on a fragment, with all living specimens collected at depths greater than 500 m. Live collected specimens are overgrown by zoanthid anemones along their dorsal and lateral surfaces (pl. 1, fig. 7). Although the vast majority of the 27 specimens examined have repaired breaks along the outer lip of the siphonal canal, only one has evidence of being drilled by naticids, suggesting that anemones may confer protection from predation by naticids. Rectal contents include polychaete setae.

Material examined:

SW of Imperieuse Reef, Rowley Shoals, Western Australia, 18°05'S, 118°10'E, in 400-401 m, mud (WAM 3259-83); SW of Imperieuse Reef, Rowley Shoals, WA, 18°01'S, 118°13'E, in 450-452 m, mud (WAM 3268-83); NW of Beagle Bay, WA, 15°08.6'S, 121°03.4'E to 15°06.0'S, 121°06.6'E, in 504-500 m, soft bottom (WAM 1089-84, holotype: WAM 1617-84, USNM 859030, paratypes); NW of Cape Leveque, WA, 14°39.5'S, 121°28.5'E to 14°41.9'S, 121°25.0'E, in 500-506 m, soft bottom (WAM 1095-84); NW of Collier Bay, WA, 13°44'S, 122°13.3'E to 13°22.3'S, 122°14.7'E, in 496-494 m, soft bottom (WAM 1656-84); W. of Cape Leveque, WA, 16°09.5'S, 120°08.8'E to 16°07.6'S, 120°10.0'E, in 600-596 m (WAM 1697-84); W of Cape Leveque, WA, 16°08'S, 120°19.5'E to 16°06.4'S, 120°20.5'E, in 550-544 m, soft bottom (WAM 1735-84); W of Cape Leveque, WA, 16°09.5'S, 120°08.8'E to 16°07.6'S, 120°10.0'E, in 600-596 m, soft bottom (WAM 1740-84); WNW of Lacepede Archipelago, WA, 15°51.2'S, 120°44.3'E to 15°49.3'S, 120°45.3'E, in 350-348 m, soft bottom (WAM 1788-84); W of Broome, WA, 17°59'S, 118°11'E to 18°11'S, 118°08'E, in 530-560 m (WAM 1807-84); W of Broome, WA, 17°59'S, 118°11'E to 18°01'S, 118°08'E, in 530-560 m, soft bottom (WAM 1809-84); NW of Collier Bay, WA, 13°50.3'S, 122°18.5'E to 13°53.4'S, 122°16.7'E, in 452-450 m, thick mud (WAM 928-85).

Comparative remarks:

Coluzea aapta may be readily differentiated from the closely related *C. distephanotis* by its double row of peripheral spines, thinner shell, longer siphonal canal and lack of a double keel. *Fulgurifusus (Histicosceptrum) xenismatis* Harasewych, 1983, from the western Caribbean Sea, also has a double row of peripheral spines, but is smaller, heavier, and has coarser spiral sculpture.

***Coluzea icarus* new species**

Plate 2, figs 1, 2; Plate 3, fig. 2

Description**Shell:**

Large (to 64 mm), moderately heavy, fusiform; spire angle 33°-37°; protoconch of 1½ whorls eroded; transition to teleconch indistinct, marked first by axial nodes, then, within ½ whorl, by spiral cords above and below periphery; cords decreasing in prominence with increase in shell size; teleconch with up to 10½ convex whorls; suture adpressed; area between suture and periphery smooth on body whorl; spiral sculpture of 1-2 weak cords between periphery and anterior carina, 2-3 weak cords between anterior carina and siphonal canal, 16-22 spiral cords along siphonal canal, with 0-3 very fine threads between adjacent cords; axial sculpture of 10-12 nodes on early whorls developing into long, broad, open spines along periphery in later whorls; aperture ovate; outer lip thin, furrowed beneath periphery; inner lip smooth, porcellaneous; siphonal canal long, axial, stout, straight to slightly sinuate distally; shell color uniformly white; periostracum axially bladed, straw-colored, thin.

Animal:

Rehydrated soft parts of holotype (WAM 1784-84) of about 2½ whorls, with mantle cavity extending over ¾ whorl, kidney ½ whorl, digestive gland nearly 1 whorl; operculum lenticular, amber colored, with terminal nucleus; proboscis long, folded in proboscis sheath; radular ribbon (pl. 3, fig. 2) small, with 104 rows of teeth; rachidia tricusped, with laterally expanded basal plates; laterals scythe-shaped.

Etymology:

Icarus, son of Daedalus.

Type material:

Holotype — WAM 1784-84, length 61.5 mm; paratypes 1 and 2, USNM 859031, lengths 63.5 mm, 55.9 mm; paratypes 3-7, WAM 1784-84, lengths 60.4 mm, 58.8 mm, 57.3 mm, 57.1 mm, 50.1 mm.

Type locality:

NW of Augustus Island, Western Australia. 13°17.0'S, 122°37.4'E to 130°18.0'S, 122°35.8'E, in 494-484 m.

Distribution (fig. 1):

Coluzea icarus has been collected along the upper continental slope off northern Western Australia at depths from 448-592 m (\bar{x} = 510 m, n = 3).

Ecology:

This species is known from three stations, all soft bottom, at depths from 448-592 m. Nearly all of the 12 specimens had repaired shell breaks, but none were drilled by naticids or muricids. Several specimens supported one or more dried anemones, which may account for lack of drilling predation. Rectum contained polychaete setae.

Material examined:

NW of Beagle Bay, Western Australia 15°09.4'S, 121°05.5'E to 15°11.4'S, 121°03.8'E, in 450-448 m, soft bottom (WAM 1611-84); NW of Augustus Island, WA, 13°17.0'S, 122°37.4'E to 13°18.0'S, 122°35.8'E, in 494-484 m, soft bottom (WAM 1784-84 — holotype, paratypes 3-7; USNM 859031 paratypes 1, 2); 154 nautical miles NW of Port Hedland, WA, 18°45.0'S, 116°26.5'E to 18°45.0'S, 116°22.5'E, in 590-592 m, mud (WAM 927-85).

Comparative remarks:

This species most closely resembles *C. distephanotis*, from which it may be distinguished by its thinner shell, finer spiral sculpture, fewer broader spines as well as by its lack of a double keel. *Coluzea icarus* is also similar to *Coluzea eastwoodae* (Kilburn, 1971) from off southeast Africa, but that species has a greater spire angle, a more steeply sloping shoulder and a thicker shell.

***Coluzea liriopae* new species**

Plate 2, figs 3, 4; Plate 3, fig. 5

Description:

Shell:

Of moderate size (to 42 mm); thin, fusiform; spire angle 43°-51°; protoconch unknown; transition to teleoconch gradual, marked by sequential appearance of peripheral keel, axial ribs, and spiral cords above and below periphery; teleoconch with up to 8 whorls; suture adpressed; spiral sculpture of 3-5 threads or cords between suture and periphery on early whorls; cord adjacent to suture increases in prominence, forming rim of sutural canal by fifth post nuclear whorl; 4 strong cords between periphery and juncture of siphonal canal; 10-12 strong cords along proximal $\frac{2}{3}$ of siphonal canal; axial sculpture of 13-15 ribs/whorl on early whorls becoming low, closed spines along periphery and nodes along first cord below periphery in later whorls; aperture ovate; outer lip thin, furrowed beneath periphery and major cords; inner lip smooth; siphonal canal long, stout, axial; shell color uniformly white; periostracum thin, yellowish, axially bladed.

Animal:

Soft parts of holotype (ZMUC) examined. Mantle cavity spans $\frac{3}{4}$ whorl, kidney $\frac{1}{2}$ whorl, upper whorls not preserved; foot broad, squarish; operculum ovate, amber-colored, with terminal nucleus; tentacles short, blunt; eyes absent or unpigmented; mantle edge thick, strongly papillose; osphradium long, broad (L/W = 2.6) with 53 filaments/side; ctenidium 1.25 as wide as osphradium, 1.5 times as long; hypobranchial gland large, transversely pleated; rectum long, narrow; anal gland along anterior $\frac{1}{2}$ rectum; extended proboscis about $\frac{2}{3}$ shell length; radula (pl. 3, fig. 5) with 120 rows of teeth; rachidia tricusped, with expanded basal plates; lateral teeth monocusped; salivary glands and Leiblein as in preceding species; female reproductive system poorly developed, with flaccid bursa copulatrix and capsule gland.

Etymology:

Gr. *Liriopae*, a fountain-nymph, mother of Narcissus.

Type material:

Holotype — ZMUC, length 41.9 mm; Paratype — MNHN, Paris, length 27.0 mm.

Type locality:

SW Makassar Strait, 3°25'S, 117°03'E, in 585 m, dark clay bottom.

Distribution:

This species has been taken at 2 stations, both in the Makassar Strait, at depths of 585 and 595 m.

Ecology:

Coluzea liriopae inhabits dark clay bottoms at depths of 585–595 m. Both specimens have repaired shell breaks, neither has been drilled. Gut contents include polychaete setae, foraminiferal tests and gastropod larval shells. It is unlikely that this species eats forams and gastropods, rather these tests probably lined tubes of ingested polychaetes.

Material examined:

SW Makassar Strait, 3°25'S, 117°03'E, in 585 m, dark clay bottom, *Galathea* station 470 (Zoological Museum, holotype); NW Makassar Strait, 00°31'N, 117°50'E, in 595 m, *Corindon* station CH214 (Museum National d'Histoire Naturelle, Paris).

Comparative remarks:

This distinctive new species may be readily distinguished from all other members of the genus by its broad, high-rimmed sutural canal and its tuberculate periphery. It somewhat resembles *C. aapta*, but with the aperture expanded in the region of the double spines.

***Coluzea gomphos* new species**

Plate 2, figs 5, 6

Description:**Shell:**

Of moderate size (to 50 mm), thin, fusiform; spire angle 49°–59°; protoconch unknown; teleoconch with sequential appearance of peripheral keel, axial ribs, spines along periphery, spiral sculpture; teleoconch with up to 7 whorls; suture adpressed; spiral thread adjacent to suture increasing in prominence to form rim of sutural canal by fifth post-nuclear whorl; 6 strong spiral cords between periphery and siphonal canal, and 8–13 along proximal $\frac{2}{3}$ of siphonal canal, with 0–1 fine threads between adjacent cords; axial sculpture limited to 11–13 flat, closed spines/whorl; aperture ovate; outer lip thin, furrowed beneath sutural rim and periphery; inner lip smooth; siphonal canal long, thin, straight; shell color uniformly white; periostracum yellowish, axially bladed; soft parts unknown.

Etymology:

Gr. *gomphos* — a large, wedge-shaped nail. Named for its broad, flat spines.

Type material:

Holotype — ANSP 291383, length 22.2 mm; paratype 1 — USNM 859032, length 25.5 mm; Paratypes 3 and 4, ANSP 291969, lengths 32.8 mm, 43.2 mm.

Type locality:

75 miles ESE of Phuket Island, Thailand, 07°40'N, 97°08'E, in 512–503 m.

Distribution:

This species inhabits the upper continental slope along the eastern Andaman Sea, at depths of 384–512 m (\bar{x} = 446 m, n = 2).

Ecology:

Four hermit crab inhabited specimens were taken at two stations, at depths of 384 m and 512–503 m. All have repaired shell breaks, one was drilled by a naticid.

Material examined:

Anton Bruun sta. 17, 75 miles ESE of Phuket Island, Thailand, 07°40'N, 97°08'E, in 512–503 m, green-brown clay (ANSP 291383, holotype; USNM 859032, paratype); Anton Bruun sta. 23, 77 miles W of Clara Island, Burma, 10°39'N, 96°35'E, in 384 m (ANSP 291969, paratypes).

Comparative remarks:

Coluzea gomphos most closely resembles *C. liriopae*, from which it differs in having a lower spire, a thinner shell with long broad spines along the periphery, and less prominent spiral sculpture. It superficially resembles *Fulgurofusus (Histricosceptrum) canaliculatus* (Martens, 1901) from off east Africa, but that species has a much thicker, more heavily sculptured shell with a higher spire and coarser periostracum.

PHENETICS

Figure 2 illustrates phenograms produced by UPGMA and single linkage clustering of the data in table 2. Both produce identical topologies for the eastern Indian Ocean species, and differ only in the linkage of the Recent New Zealand species (*C. spiralis*) to the Paris Basin Eocene species (*C. serrata*) [UPGMA] or to the Recent Indian Ocean species [single linkage]. This difference between the phenograms would be eliminated if they were unrooted. Interpreted as phylogenies, they would indicate that the Indian Ocean species are part of a monophyletic radiation that occurred subsequent to the separation of the Pacific taxa, of which *C. spiralis* serves as exemplar.

Table 2. Measurement of shell characters in the format Mean/Standard Deviation. All linear measurements in mm. Mean values constitute the data matrix for phenetic analyses.

Character	<i>distephanotis</i> n=5	<i>aapta</i> n=5	<i>icarus</i> n=5	<i>liriopae</i> n = 2	<i>gomphos</i> n=4	<i>spiralis</i> n=2	<i>serrata</i> n=2
1. Sbc	1.48/0.14	1.43/0.13	1.49/0.06	1.34/0.08	1.40/0.07	1.52/0.12	1.89/0.07
2. Ssc	22.7/5.8	26.1/1.5	20.9/3.3	23.2/2.1	20.8/4.5	19.1/2.8	21.4/3.0
3. Rsl	3.20/0.37	3.81/0.22	2.80/0.42	2.98/0.34	2.82/0.78	2.91/0.12	2.27/0.03
4. beta	25.8/4.1	27.3/3.4	24.8/1.7	27.2/0.8	24.9/3.5	20.5/2.5	18.8/2.7
5. theta	29.4/4.1	30.3/3.2	28.6/1.9	33.0/0.0	30.1/3.2	24.5/2.0	21.2/1.8
6. W	1.38/0.02	1.34/0.03	1.31/0.02	1.44/0.03	1.55/0.03	1.38/0.02	1.36/0.02
7. D	0.218/0.049	0.215/0.044	0.209/0.044	0.257/0.030	0.208/0.040	0.206/0.040	0.161/0.050
8. T	6.33/0.85	6.55/0.48	6.49/0.73	4.65/0.04	4.40/0.59	5.79/0.33	7.58/0.70
9. # var	13.8/1.0	14.0/0.9	11.4/0.8	14.0/1.0	12.0/1.0	16.5/0.5	10.0/0.0
10. rim	0.000/0.000	0.224/0.030	0.000/0.000	0.597/0.003	0.664/0.010	0.000/0.000	0.000/0.000
11. color	1.0	1.0	1.0	1.0	1.0	0.0	0.0
12. spines	1.0	1.0	1.0	0.0	0.0	0.0	0.0

DISCUSSION

The gross anatomy of the eastern Indian Ocean Columbariinae agrees in most respects with that of the western Atlantic species (Harasewych, 1983). Nevertheless, the Indian Ocean species differ in having: eyes that are greatly reduced or absent; a thickened mantle edge; a narrower osphradium with more numerous leaflets; a ctenidium that is broader than the osphradium; a deeper, more glandular hypobranchial gland; and radulae that are larger, proportionally longer, and have more rows of teeth. Additional material from the western Indian and southwestern Pacific Oceans is required to determine which of these differences are ecologically mediated, and which may serve to differentiate the genera *Coluzea* and *Fulgurofusus*.

Figure 2 illustrates the phenetically deduced relationships between the taxa. Cladistic analyses were not included because of difficulties in differentiating between homologies, atavisms and convergences.

The three species occurring off northwestern Australia are closely related, but differ in their bathymetric distributions. Triplets of closely related species with similar geographic distributions but differing bathymetric ranges also occur in the western Atlantic [*Fulgurofusus (Peristarium)*].

aurora, *F. merope*, *F. electra* (Bayer, 1971; Harasewych, 1983)] and western Indian [*Coluzea radialis*, *C. rotunda*, *C. angularis* (Barnard, 1959)] Oceans, suggesting the possibility that such bathymetric speciation may be a result of sea level changes during the Cenozoic (Vail et al., 1977).

The eastern Indian Ocean species are more closely related to elements of the western Indian Ocean columbarine fauna than to their congeners from the Recent of New Zealand. Among the New Zealand species of *Coluzea*, the greatest affinities are with the Early Miocene species *C. paucispinosa* Finlay, 1930 and *C. dentata* (Hutton, 1877). It is suggested that the divergence between at least some components of the Pacific and Indian Ocean upper continental slope faunas occurred between the time of the shift of the Columbariinae to the psychrosphere (Late Eocene/Oligocene) and the Early Miocene, and is due to vicariance.

ACKNOWLEDGEMENTS

I thank Dr. F.E. Wells of the Western Australian Museum, Dr. Robert Robertson of the Academy of Natural Sciences of Philadelphia, Dr. P. Bouchet of the Museum National d'Histoire Naturelle, Dr. J. Knudsen of the Zoological Museum, Copenhagen, Dr. M.V. Hounscome of the Manchester Museum, Dr. C.P. Nuttall of the British Museum (Natural History) and Mr. R.H. Jensen of the Delaware Museum of Natural History for making available the specimens on which this study was based.

Photographs are by Mr. V. Krantz, photographic services, National Museum of Natural History, Smithsonian Institution. The assistance of Ms. S. Braden on the scanning electron microscope is gratefully acknowledged.

I am indebted to Dr. M.F. Mickevich for access to and assistance with PHYSYS, and to Drs. R.S. Houbbrick and R. Hershler, National Museum of Natural History, Smithsonian Institution, for critical readings of drafts of the manuscript.

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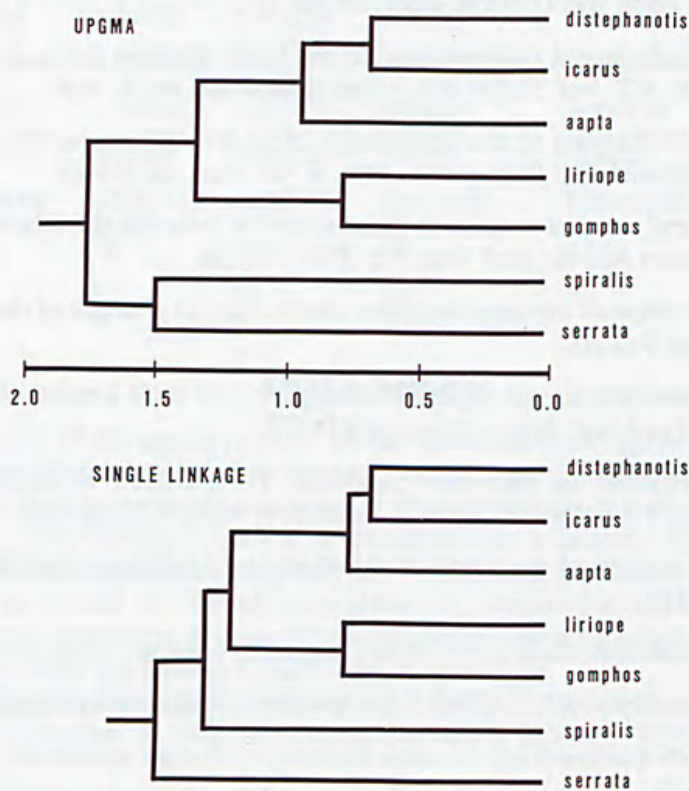


Figure 2. Phenograms resulting from UPGMA (upper) and Single Linkage (lower) clustering of Euclidian distances using standardized data.



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